



Chemical Ecology and Sociality in Aphids: Opportunities and Directions

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Abstract

Aphids have long been recognized as good phytochemists. They are small sap-feeding plant herbivores with complex life cycles that can involve cyclical parthenogenesis and seasonal host plant alternation, and most are plant specialists. Aphids have distinctive traits for identifying and exploiting their host plants, including the expression of polyphenisms, a form of discrete phenotypic plasticity characteristic of insects, but taken to extreme in aphids. In a relatively small number of species, a social polyphenism occurs, involving sub-adult “soldiers” that are behaviorally or morphologically specialized to defend their nestmates from predators. Soldiers are sterile in many species, constituting a form of eusociality and reproductive division of labor that bears striking resemblances with other social insects. Despite a wealth of knowledge about the chemical ecology of non-social aphids and their phytophagous lifestyles, the molecular and chemoeological mechanisms involved in social polyphenisms in aphids are poorly understood. We provide a brief primer on aspects of aphid life cycles and chemical ecology for the non-specialists, and an overview of the social biology of aphids, with special attention to chemoeological perspectives. We discuss some of our own efforts to characterize how host plant chemistry may shape social traits in aphids. As good phytochemists, social aphids provide a bridge between the study of insect social evolution sociality, and the chemical ecology of plant-insect interactions. Aphids provide many promising opportunities for the study of sociality in insects, and to understand both the convergent and novel traits that characterize complex sociality on plants.

Keywords Aphids · Sociality · Chemical ecology · Polyphenisms · Fatty acids

Introduction

The evolution of social behavior stems from group coordination of activities such as offspring care, resource acquisition, and defense (Bourke 2011; Ward and Webster 2016). In insects, group coordination occurs via various sensory channels, with chemical modes of particular importance (Hölldobler and Wilson 2008; Leonhardt et al. 2016). Social Hymenoptera and higher termites construct nests, forage for food, and provision offspring, and the behavioral complexity of these tasks requires elaborate means of communication (Camazine et al.

2002; Fewell and Abbot 2017; Korb and Heinze 2016). Given its centrality to understanding how social insects organize their societies, the chemical ecology of ants, bees and termites has long been an object of inquiry, and with new tools emerging in recent years, is a burgeoning field (e.g., Tribble et al. 2017; Yan et al. 2017). Much less is known, however, about the chemical basis of social organization of other social or solitary insects, and there is much left to learn about the origins and generality of chemoeological patterns across the full breadth of social insects.

In this paper, we highlight some of the general features of the chemical ecology of aphids and how chemical communication may have influenced evolution of social behavior in aphids. Aphids (Hemiptera: Aphidoidea: Aphididae) are small sap-feeding insect herbivores. In a small fraction of species, family groups occur with patterns of social organization resembling that of ants, bees and termites (Abbot 2015; Abbot and Chapman 2017; Stern and Foster 1996). Family groups begin with the stem mother forming the nest and reproducing clonally within the nest. Their characteristic features are castes of juvenile soldiers that defend their colony from predators and parasites. While functional studies on social evolution in

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aphids are emerging (Shibao et al. 2010, 2016), by and large, the regulation and functional biology of social groups remain poorly understood in social aphids, and there are many outstanding questions. What chemoecological traits facilitate production of specialized soldier castes? What mechanisms underlie expression of aggressive, even lethal, nymphs in otherwise small and timid sap-feeding herbivores? There are good prospects for answering such questions, because aphids and their allies are models for understanding plant-insect interactions, the developmental basis of insect polyphenisms, and interactions among insects and microbial and viral mutualists and pathogens (Brisson and Stern 2006; Moran et al. 2008; Srinivasan and Brisson 2012; Tagu et al. 2010). The wealth of information on how aphids regulate development and respond to conspecifics, host plants, and predators provide a largely untapped resource for studying developmental and chemical bases of sociality. Our goal in this paper is to provide a general overview of aphid life history and sociality. We highlight various examples of chemoecological studies of social aphids, including some preliminary work we have done on fatty acid variation in social and non-social species and their host plants, that together point to promising directions for future study.

Aphid Life Cycles: the Starting Point for Aphid Sociality

It can be challenging to appreciate sociality in aphids without some familiarity with the life cycles and polyphenisms of aphids; therefore, the following brief primer will provide helpful context. Variation in aphid life cycles is organized around patterns of host-plant use and mode of reproduction (Moran 1992). Most aphids specialize on one or a group of related host-plant species (Peccoud et al. 2010). However, in about 10% of aphid species, seasonal alternation occurs between unrelated host-plant species (*heteroecy*), encompassing a primary, typically woody-host species where the sexual and overwintering generations occur, and one or several secondary host plants, where only parthenogenetic reproduction occurs. Aphids life cycles incorporate a sexual phase between bouts of apomictic parthenogenesis (a complete life cycle or *holocycle*). Some species have secondarily lost the sexual phase (i.e., they do not produce males; *anholocycle*), or else sexual generations have not yet been identified. Life cycle plasticity is common in aphids, and complex patterns of complete and incomplete life cycles can be expressed within a single species (Simon et al. 2010). For example, aphids can persist at higher latitudes by way of cold-hardy, sexually produced eggs that survive winters. However, in warmer climates or in areas where their primary hosts are rare, a sexual generation may not occur and they may overwinter as mobile nymphs or adults. Thus, in some species, there are distinct

biogeographic and temporal patterns in modes of reproduction (Guillemaud et al. 2003).

Polyphenisms, or the expression of discrete, environmentally cued phenotypes, allow for non-evolutionary adaptation to predictable patterns of environmental variation (Davis 2012; Nijhout 2003; Simpson et al. 2011). Aphids express diverse types of phase, dispersal and reproductive polyphenisms, encompassing up to eight or nine morphs (Moran 1992). These include sexual morphs and various kinds of winged or wingless viviparous, parthenogenetic females, or viviparae (Braendle et al. 2006). In holocyclic species, the foundress or stem mother is a viviparous parthenogenetic female derived from a sexually produced egg. Many host alternating species induce tumor-like galls on their host plants (Wool 2004). Galls are initiated by the asexually-reproducing foundress, nearly always on the primary host-plant, and only rarely on the secondary host (Akimoto et al. 1996). Polyphenisms are particularly pronounced in gall-inducing aphids, because of the seasonal and plant-associated heterogeneity implied by their holocyclic, heteroecious life cycles, as well as that accompanying gall induction itself. Consider the life cycle of *Paraclletus cimiciformis* (Aphididae: Eriosomatinae: Fordini), a gall-inducing species that expresses nine morphs on two host plants. *P. cimiciformis* expresses not only the sexual and gall-associated morphs on its primary host and secondary host morphs, but includes a color polymorphism on its secondary hosts, one of which parasitically feeds upon the eggs of its mutualistic ant host (Salazar et al. 2015).

Sociality in Aphids: Fortress Defense in Sap-Feeding Insects

Most aphids are not social, and most social species are confined to two small subfamilies within Aphididae (Hormaphidinae and Eriosomatinae), and in these, sociality is labile, with evidence of multiple origins and losses (Stern 1994, 1998; Table 1). While most gall-inducing species in the Hormaphidinae and Eriosomatinae are not social, all aphids that are social induce galls. Multiple origins of sociality means that many social species are closely related to species that are not social, making aphids valuable for comparative studies of insect social evolution (Abbot and Chapman 2017; Stern and Foster 1996).

Aoki (1976) described the first social aphid a little more than 40 years ago. Since then, about 60 or so species of aphids have been described as eusocial (Abbot 2015; Abbot and Chapman 2017; Aoki and Kurosu 2010; Pike et al. 2007; Stern and Foster 1996). Generalizing, a viviparous, wingless asexual adult (the “queen” in social insect parlance) initiates a group of one or more generations of her lineage in which, at some point, a caste of nymphal soldier develops (Stern and

Table 1 A partial list of social aphid species, their primary and/or secondary hosts, and whether soldiers occur on the primary (P) or secondary (S) host plant as 1st (1), 2nd (2) instar nymphs, 4th (4) instar, or adults (A). A: Aphidinae; H: Hormaphidinae; E: Eriosomatinae

Species	Taxonomy	Primary host	Secondary host plant	P	S
<i>Astegopteryx bambucifoliae</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Poaceae</i>	1, 2	1
<i>Astegopteryx spinocephala</i>	H: Cerataphidini	<i>Styrax benzoides</i>	–	2	
<i>Astegopteryx styracicola</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Zingiberaceae</i>	2	
<i>Cerataphis fransseni</i>	H: Cerataphidini	<i>Styrax benzoin</i>	<i>Palms</i>	2	
<i>Cerataphis jamuritsu</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	–	2	
<i>Cerataphis vandermeermohri</i>	H: Cerataphidini	<i>Styrax serrulata</i>	–	2	
<i>Ceratoglyphina bambusae</i>	H: Cerataphidini	<i>Styrax benzoin</i>	<i>Gramineae</i>	2	
<i>Ceratoglyphina styracicola</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Pleioblastus</i>	1, 2	
<i>Ceratovacuna cerbera</i>	H: Cerataphidini	–	<i>Sasa spp.</i>		1
<i>Ceratovacuna japonica</i>	H: Cerataphidini	<i>Styrax japonicus</i>	<i>Poaceae</i>	2	1
<i>Ceratovacuna lanigera</i>	H: Cerataphidini	–	<i>Andropogoneae</i>		1
<i>Ceratovacuna nekoashi</i>	H: Cerataphidini	<i>Styrax japonicus</i>	<i>Microstegium spp.</i>	2	
<i>Ceratovacuna oplismeni</i>	H: Cerataphidini	<i>Styrax spp.</i>	<i>Microstegium spp.</i>	2	
<i>Ceratovacuna orientalis</i>	H: Cerataphidini	<i>Styrax formosanus</i>	<i>Microstegium spp.</i>	2	
<i>Ceratovacuna subtropicana</i>	H: Cerataphidini	<i>Styrax formosanus</i>	<i>Microstegium spp.</i>	2	1
<i>Colophina arma</i>	E: Eriosomatini	<i>Zelkova serrata</i>	<i>Clematis stans</i>	1, 2	1
<i>Colophina clematicola</i>	E: Eriosomatini	<i>Zelkova spp.</i>	<i>Clematis terniflora</i>	1	1
<i>Colophina clematis</i>	E: Eriosomatini	<i>Zelkova serrata</i>	<i>Clematis apiifolia</i>	1, 2	1
<i>Colophina monstifera</i>	E: Eriosomatini	?	<i>Clematis floribunda</i>		1
<i>Dinipponaphis autumnae</i>	H: Nipponaphidini	<i>Distylium racemosum</i>	–	1	
<i>Distylaphis foliorum</i>	H: Nipponaphidini	<i>Distylium stellare</i>	–	1	
<i>Epipemphigus niisimae</i>	E: Pemphigini	<i>Populus maximowiczii</i>	<i>Balsaminaceae</i>	1	
<i>Eriosoma morioense</i>	E: Eriosomatini	<i>Ulmus spp.</i>	<i>Sedum spp.</i>	2, 3	
<i>Grylloprociphilus imbricator</i>	E: Pemphigini	<i>Fagus grandifolia</i>	<i>Taxodium distichum</i>	4	
<i>Hamamelistes kagamii</i>	H: Hormaphidini	<i>Hamamelis japonica</i>	<i>Betula grossa</i>	1	
<i>Hamamelistes miyabei</i>	H: Hormaphidini	<i>Hamamelis japonica</i>	<i>Betula maximowicziana</i>	1	1
<i>Hemipodaphis persimilis</i>	E: Eriosomatini	<i>Zelkova serrata</i>	?	1	
<i>Indonipponaphis fulvicola</i>	H: Nipponaphidini	<i>Distylium racemosum</i>	<i>Quercus spp.</i>	1	
<i>Nipponaphis distyliicola</i>	H: Nipponaphidini	<i>Distylium racemosum</i>	<i>Quercus spp.</i>	1	
<i>Nipponaphis monzeni</i>	H: Nipponaphidini	<i>Distylium racemosum</i>	<i>Quercus spp.</i>	1	
<i>Paracolopha morrisoni</i>	E: Eriosomatini	<i>Zelkova serrata</i>	<i>Sasa spp.</i>	1	
<i>Pemphigus bursarius</i>	E: Pemphigini	<i>Populus nigra</i>	<i>Asteraceae</i>	1	
<i>Pemphigus dorocola</i>	E: Pemphigini	<i>Populus maximowiczii</i>	?	1	
<i>Pemphigus gairi</i>	E: Pemphigini	<i>Populus nigra</i>	<i>Apiaceae</i>	1	
<i>Pemphigus monophagus</i>	E: Pemphigini	<i>Populus spp.</i>	–	1	
<i>Pemphigus obesinymphae</i>	E: Pemphigini	<i>Populus spp.</i>	<i>Brassicaceae</i>	1	
<i>Pemphigus phenax</i>	E: Pemphigini	<i>Populus nigra</i>	<i>Daucus spp.</i>	1	
<i>Pemphigus populitransversus</i>	E: Pemphigini	<i>Populus deltoides</i>	<i>Brassicaceae</i>	1	
<i>Pemphigus protospirae</i>	E: Pemphigini	<i>Populus spp.</i>	<i>Umbelliferae</i>	1	
<i>Pemphigus spyrothecae</i>	E: Pemphigini	<i>Populus nigra</i>	–	1	
<i>Pseudoregma alexanderi</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Bambuseae</i>		1
<i>Pseudoregma baenzigeri</i>	H: Cerataphidini	<i>Styrax spp.</i>	<i>Dendrocalamus sp.</i>	?	1
<i>Pseudoregma bambucicola</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Poaceae</i>	2	1
<i>Pseudoregma koshunensis</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Poaceae</i>	2	1
<i>Pseudoregma nicolaiae</i>	H: Cerataphidini	<i>Styrax spp.</i>	<i>Zingiberaceae</i>	?	1
<i>Pseudoregma panicola</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Oplismenus spp.</i>	2	1
<i>Pseudoregma shitosanensis</i>	H: Cerataphidini	<i>Styrax suberifolia</i>	<i>Poaceae</i>	2	1
<i>Pseudoregma sundanica</i>	H: Cerataphidini	<i>Styrax spp.</i>	<i>Zingiberaceae</i>	2	1

Table 1 (continued)

Species	Taxonomy	Primary host	Secondary host plant	P	S
<i>Quadrartus yoshinomiya</i>	H: Nipponaphidini	<i>Distylium racemosum</i>	<i>Quercus acutissima</i>	1	
<i>Smynthuroides betae</i>	E: Fordini	<i>Pistachia</i> spp.	Asteraceae	A	
<i>Tamalia cowenii</i>	A: Tamalinae	<i>Arctostaphylos</i> spp.	–	–	–
<i>Tuberaphis coreana</i>	H: Cerataphidini	<i>Styrax formosana</i>	Loranthaceae	2	
<i>Tuberaphis leeuweni</i>	H: Cerataphidini	<i>Styrax serrulata</i>	–	2	
<i>Tuberaphis owadai</i>	H: Cerataphidini	<i>Styrax tonkinensis</i>	–	2	
<i>Tuberaphis styraci</i>	H: Cerataphidini	<i>Styrax obassia</i>	–	2	
<i>Tuberaphis taiwana</i>	H: Cerataphidini	<i>Styrax formosana</i>	Loranthaceae	2	
<i>Tuberaphis takenouchii</i>	H: Cerataphidini	<i>Styrax</i> spp.	Loranthaceae	2	1

More complete taxonomic and social descriptions can be found in Blackman and Eastop (1994), Stern and Foster (1996), Pike et al. (2007), Aoki and Kurosu (2010)

Foster 1996). Soldiers are behaviorally and/or morphologically specialized for colony defense and other tasks, such as gall repair or waste removal (Kutsukake et al. 2009), and are usually the early juvenile stages (1st or 2nd instar nymphs). Most social aphid groups are often found within galls on the primary host-plant species, but in some species, social groups form on the secondary host plant species in the absence of galls (Fig. 1). In a handful of species, social groups can be found on both the primary and secondary host plants (Fig. 1; Table 1). The majority of social species in the Hormaphidinae occur within a single tribe, the Cerataphidini, which has a tropical distribution centered on South-East Asia (Aoki and Kurosu 2010). Species in the

Cerataphidini alternate between trees in the silverbell family (Styracaceae: *Styrax* spp.), and diverse secondary hosts, including various bamboo, palms, and gingers. The Cerataphidini produce sterile 2nd instar soldiers within galls on their primary host and some produce 1st instar soldiers, as well (Aoki and Kurosu 2010). *Tuberaphis styraci* has been the focus of study among the Cerataphidini because it is monoecious, which has facilitated development of protocols for lab-based cultures on artificial diets and functional work (Shibao et al. 2002, 2004a, b, 2010, 2016). In the Eriosomatinae, most social species are found in the tribe Pemphigini, which include both heteroecious and monoecious species that induce galls on poplars (Salicaceae: *Populus* spp.), within which either monomorphic or dimorphic 1st instar soldier castes develop. Secondary host soldiers have not been described in the Pemphigini, but in the related Eriosomatini, *Colophina* spp. form soldiers on both primary and secondary hosts (Table 1).

The sociality that aphids express has been characterized as “fortress defense”, because their division of labor involves production of sterile soldiers that defend their kin from predators and parasites, rather than the workers typical of social Hymenoptera (Crespi 1994; Korb and Heinze 2008, 2016; Queller and Strassmann 1998). They share similarities with hemimetabolous wood-dwelling termites and eusocial thrips, and some other cavity-nesting insects, which also form social groups in or on their food (Korb and Thorne 2017). By contrast, all social Hymenoptera and higher termites construct nests or forage outside of their nests for food, and directly provision offspring within groups. The difference between the two types of social insects – both in development and the essential features of their societies with respect to nest construction, food acquisition, and offspring care - is almost certainly reflected in differences in the chemoecological social traits. The higher eusocial insects exhibit diverse traits for generating and perceiving pheromones and other chemical signals (Hölldobler and Wilson 2008). Like solitary insects, social insects use cuticular hydrocarbons (CHCs, including

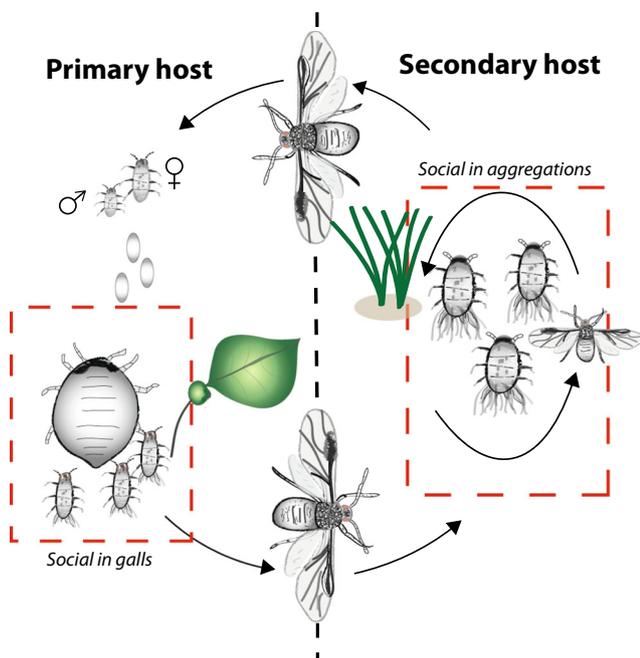


Fig. 1 A generalized life cycle of a heteroecious, holocyclic eriosomatine life cycle, in which soldiers are found on both primary and secondary host plants

various blends of *n*-alkanes, alkenes, methyl-branched alkanes) in both interspecific and sexual interactions (Kocher and Grozinger 2011). Social insects also actively secrete pheromones and other volatile and non-volatile semiochemicals, by way of a diverse set of exocrine glands (Billen and Sobotnik 2015). Signal reception is equally elaborate in the social Hymenoptera and termites; odorant receptors are dramatically expanded in ants, for example (Zhou et al. 2012). By contrast, comparatively few generalities of these sorts can be made for social aphids and their allies (Table 2).

In sum, sociality in aphids involves expression of a unique polyphenism (soldiers) in gall-inducing species with complex life cycles, and represents an alternative mode of insect sociality. Below, we map out some of the features of the chemical ecological world that aphids occupy. Some may prove to have little to do directly with sociality in aphids, but because so little is known, it is too soon to say. And there are good reasons to suspect they are. For example, one of the clear phenotypic correlates of sociality in aphids is the developmental extension of the larval soldier stage – the developmental rate of soldiers is slower, even arrested, in social aphids (Pike et al. 2004). Conversely, in some species, soldier development can be accelerated in some circumstances: by the presence or absence of the foundress, or when soldiers move between groups (Abbot et al. 2001; Withgott et al. 1997). Aphid soldiers express clear evidence of developmental plasticity, and while the mechanisms are unknown, both social and non-social aphids probably share related mechanisms. Moreover, gall induction itself may predispose species to sociality by providing developmental, chemical or behavioral pre-adaptations for soldier evolution (Abbot 2015; Kutsukake et al. 2009, 2012; Lawson et al. 2017). Social behavior is thus intimately tied to how aphids develop on and interact with their host plants.

Aphid Chemical Ecology: Sociality at the Plant-Insect Interface

Herbivory Like all herbivorous insects, aphids must successfully locate and exploit their host plants by responding to signals that cue developmental transitions, and by expressing traits that facilitate acquisition of nutritionally suitable diets and circumvent host-plant defenses (Behmer 2008; Brisson and Davis 2016; Nishida 2014). Aphids feed on phloem in sieve elements of their host plants. Phloem contains an array of macromolecules involved in plant growth, development, and defense, including hundreds of secondary metabolites, proteins, peptides, nucleic acids, mRNAs, free and conjugated fatty acids, lipids and various transcripts and small RNAs (Atkins et al. 2011). Plants can respond to aphid feeding by up-regulating phytohormone-based resistance pathways (principally salicylates or jasmonates) as well as various lipids and fatty acids (De Vos and Jander 2009; Kachroo and Kachroo

2009; Smith et al. 2010; Tooker and Helms 2014). Aphids can manipulate their host plants to improve host-plant nutrition and/or decrease plant defenses. These manipulations, which include gall induction, likely involve effectors that alter host-plant physiology to the benefit of the aphids (Cao et al. 2016; Elzinga and Jander 2013; Elzinga et al. 2014; Kim and Jander 2007).

Host Location and Feeding Although aphids can walk between host plants, dispersal and host-plant colonization characteristically involves development of specialized winged migrants (Blackman and Eastop 1994). Aphids are poor flyers with little directional control, and the behavioral challenges of migrating aphids are typically divided into host location and host recognition (Döring 2014; Powell et al. 2006). Aphids have olfactory organs on their antennae, as well as chemo- and mechanoreceptors on tarsi and proboscis or maxillary palps that respond to both volatile and non-volatile plant cues (Powell et al. 2006). However, the general consensus is that, at long distances, host location initially involves either phototactic cues or blind luck (Döring 2014). It has been estimated that fewer than 1 in 100 dispersing alates successfully colonize new host plants, which gives a sense of the prodigious numerical abundances that aphid can generate (Ward et al. 1998). Aphids seem to respond to blends of both host-derived and ubiquitous volatile compounds to locate hosts (Webster 2012). These volatiles can either attract or repel, and include many of the compounds commonly recognized by herbivorous insects, including various isoprenoids and fatty acid derivatives (Bruce et al. 2005). The black bean aphid *Aphis fabae*, for example, responds to a blend of ubiquitous compounds to locate broad bean (*Vicia faba*), even though these compounds are individually repellent (Webster et al. 2010). Ultimately, aphids sample the leaf surface by penetrating the epidermis with their stylets and ingesting sap from mesophyll and parenchyma tissues, which they use to further discriminate between hosts by integrating tactile and visual cues at the leaf surface (Webster 2012). Once a host is selected, feeding involves a highly stylized mode of “intercellular foraging” in which they insert their needle-like stylets through the plant apoplast, secreting two types of watery and gel-like saliva (Simon et al. 2015; Will et al. 2013). Plant-defense responses may be suppressed by secretion of various salivary proteins and molecules, including those that mitigate reactive oxygen species (glutathione peroxidases) and prevent sieve tube occlusion by callose deposition and various proteins (e.g., Ca²⁺ binding proteins and proteases) (Will et al. 2013). Patterns of metabolic resistance to ingested plant-defensive chemistry remains poorly characterized in aphids, but include an array of canonical phase I, II and III enzymes, such as cytochrome P450s, glutathione-S-transferases (GSTs), and ATP-binding cassette (ABC) transporters (Birnbaum et al. 2017; Simon et al. 2015).

Table 2 Ten functions of communication in ants across four main categories, after Hölldobler and Wilson (2008), with analogous traits in non-social aphids and whether derived analogs are present or absent in social aphids

Category	Function in higher social insects	Chemoecological ex. in higher social insects	Non-social aphid traits	Derived example in social aphids	Aphid references
Recruitment	attraction; group formation	alcohols, aldehydes, terpenoids, lactones, isocoumarins, etc.	migrating morphs response to aphid & plant cues	unknown; galls enforce family groups	see text for non-social aphid references
	territoriality; colony home range	numerous examples	foundress territoriality; fighting	no evidence of kin recognition; social parasitism in various species	Whitham 1986; Aoki and Makino 1982; Wang et al. 2008
Response to natural enemies	alarm signals	alarm pheromones; alcohols, aldehydes, ketones, esters, hydrocarbons, terpenoids, etc.	alarm pheromone; mono and sesquiterpenes; isothiocyanates; leave plant; winged morphs	alarm pheromone stimulates attack by nymphal soldiers	Arakaki 1989
Nest-mate recognition	sharing of food or pheromones	numerous examples	absent: live within food and hemimetaboly	absent	see text for non-social aphid references
	solid food exchange	numerous examples	cannibalism	absent	Cooper et al. 2014
	coordinating group activities	pheromones	scent marking predators	soldiers scent mark predators	Mondor and Roitberg 2004; Arakaki 1989
	recognition; nestmate vs non-nestmates, kin	cuticular hydrocarbons; queen or colony-specific pheromonal signals	absent; aphid aggregations tend to be clonal b/c of reproductive mode	no evidence of kin recognition; evidence of context-dependent behaviors and development	Miller III 1998; Abbot and Chhatre 2007; Abbot et al. 2001; Aoki et al. 1991
Queen signals, division of labor	caste determination; division of labor	numerous examples	polyphenisms	developmental plasticity in soldiers; +/- density dependence	Shibao et al. 2010
	reproductive division of labor	numerous examples	cyclical parthenogenesis	cyclical parthenogenesis	see text for non-social aphid references
	sexual communication; species or gender recognition	sex pheromones	pheromonal communication between male & female sexuals	absent; all female societies	see text for non-social aphid references

Polyphenisms Because of the importance of aphids as crop pests, as well as their utility as models for understanding insect development, there is interest in characterizing how environmental cues are translated into the appropriate developmental fates in aphids (Davis 2012). Both extrinsic and intrinsic factors trigger developmental polyphenisms in aphids (Brisson 2010; Simon et al. 2010). Reproductive polyphenisms (the switch between asexual and sexual reproduction) are regulated by responses to changes in temperature-modulated photoperiod (Tagu et al. 2005). Long nights and falling temperatures cue the switch from parthenogenetic to sexual reproduction. While full signal transduction pathways for aphid polyphenisms remain to be worked out, juvenile hormone (JH-III in aphids) is thought to be a likely candidate for the regulation of reproductive mode in aphids, because of its documented role in insect polyphenisms (Braendle et al. 2006; Nijhout 2003). In the pea aphid (*Acyrtosiphon pisum*), JH-III titers are higher in aphids producing parthenogenetic morphs under long-day conditions than in those producing sexual morphs under short day conditions (Ishikawa et al. 2011), consistent with a role for JH in regulating reproductive mode in aphids.

Wing dimorphism marks key shifts in reproductive mode and host plant colonization. Outside of the winged sexual males, all winged/wingless dimorphisms are environmentally cued, and are true polyphenisms (Braendle et al. 2006). Changes in host-plant quality stimulate induction of winged morphs, because unfavorable conditions should be associated with production of individuals adapted for dispersal. However, many aphids also use tactile or chemical cues to gauge density and crowding as signals for winged morph-induction, rather than cues derived from plants themselves (Müller et al. 2001). High density treatment of aphid mothers can induce the production of winged progeny, suggesting that embryonic fate might be governed by “crowd-signaling substances” that accumulate in aphid mothers exposed to crowding (Ishikawa and Miura 2013). Predator cues can also induce the production of winged morphs (Mondor et al. 2004; Podjasek et al. 2011).

Because of viviparity, aphid morphs can be signaled prenatally (maternally or grand maternally, since aphids have telescoping generations, or the presence of multicellular embryos within the ovaries of late-stage prenatal embryos), and cues are processed not by the individuals themselves, but by their mothers or grandmothers. A combination of embryonic and post-natal cues probably determines the final developmental fate in most aphids. How signals for winged dimorphism are transduced is less clear (Müller et al. 2001). While high levels of JH have been thought to result in essentially the retention of juvenile features that result in wingless adults, there are no clear relationships between JH levels and wing dimorphisms in the species that have been studied (Braendle et al. 2006; Schwartzberg et al. 2008). Other endocrine factors

are likely also important in governing the response to environmental signals that cue reproductive polyphenisms (Gao and Hardie 1997), and recent work has shown an important role for ecdysone in winged morph determination. High levels of ecdysone, the production of which occurs in aphid ovaries and can be density-dependent, are associated with the production of wingless offspring (Vellichiramal et al. 2017). Moreover, genes associated with morph specificity in the pea aphid have distinct expression profiles, and are enriched for those involved in ecdysone regulation (Purandare et al. 2014; Vellichiramal et al. 2016).

Predator Avoidance Various species of aphids, social or not, coordinate defenses against predators. By aggregating, aphids can dilute individual risk against predators, or enhance the effectiveness of active defense behaviors such as leg-kicking or the sequestration and secretion of defensive plant chemicals. For example, the oleander aphid, *Aphis nerii*, a bright yellow aposematic aphid that specializes on milkweed and its relatives in the Apocynaceae and Asclepiadaceae families, are thought to sequester the cardenolides that milkweed produce as means of defense against herbivores (Birnbaum and Abbot 2018; Züst and Agrawal 2015). Many species in the large subfamily Aphidinae secrete an oily, sticky exudate from their cornicles (rod-like abdominal secretory structures unique to aphids) when disturbed or threatened by predators (Dixon 1998). The secretions, which rapidly harden upon touching a solid object, comprise a mixture of triglycerides, free fatty acids, organic acids, sugars (e.g., trehalose), and more rarely, amino acids (Alfaress et al. 2015). Relative fatty acid composition varies from species to species, and from morph to morph (Strong 1963), with myristic (C14:0) and palmitic (C16:0) acids being most commonly reported, and minor constituents in aphid triglycerides that including both saturated (lauric: C12:0 and stearic: C18:0) and unsaturated fatty acids (oleic: C18:1 and linoleic: C18:2) (Alfaress et al. 2015; Callow et al. 1973; Febvay et al. 1992). Despite considerable variation between species, the chemical composition of cornicle secretions reflects the body composition of aphids (Greenway and Griffiths 1973). The gall-inducing species *Quadratus yoshinomiya* exhibits a unique form of predator deterrence in which older individuals secrete a waxy substance that glues them to intruding predators (Uematsu et al. 2010). Predators are immobilized or incapacitated when the wax solidifies.

In many aphids, an additional component of exudates is an alarm pheromone, most commonly (*E*)- β -farnesene, which is a volatile sesquiterpene (Vandermoten et al. 2012). Because of clonal reproduction, aphid aggregations comprise a single or few clones (Vantaux et al. 2011), and there are likely kin-selected advantages to alerting group mates to danger (Mondor and Roitberg 2004). In some species, pheromone production depends upon group composition: pea aphids

(*Acyrtosiphon pisum*) produce more pheromone in the presence of conspecifics than when alone (Verheggen et al. 2009). Finally, mutualisms between aphids and ants are common. Aphid honeydew can provide an important source of carbohydrates in ant diets, and ants will defend their aphid hosts aggressively (Way 1963). Because mutualism with ants provides defense against predators, the presence or absence of ant mutualism may have an effect on the evolution or expression of sociality in aphids (Pike et al. 2007; Shingleton and Foster 2000).

Chemo-Ecological Perspectives on Aphid Sociality

Caste Regulation With rare exceptions, social aphid castes consist of 1st or 2nd instar soldiers that typically exhibit exaggerated morphological traits relative to normal nymphs (Fig. 1; Table 1). Because soldier castes are established at birth or early in development, prenatal effects on embryos are likely important in caste determination. In *Pseudoregma bambucicola*, a hormaphidine species that forms social groups on its secondary host (*Bambusa multiplex*), morphological traits of embryos gradually differentiate during embryogenesis to generate soldiers and normal embryos, with further differentiation after larviposition (Ijichi et al. 2004). However, post-natal effects are important as well, and likely act in concert with pre-natal cues to determine developmental fate of soldiers (Pike et al. 2004; Shibao et al. 2010). A number of studies have identified extrinsic factors that regulate soldier production and development, and density and crowding are important cues (Akimoto 1992; Hattori et al. 2013; Ijichi et al. 2005; Shibao 1999). For example, *Tuberaphis styraci* produce a caste of 2nd instar soldiers within their galls on bamboo, such that their mature colonies contain both normal and soldier-like nymphs. However, the proportion of soldiers in these colonies varies as the colonies grow, and the soldier proportion is initially low in small colonies, and higher in large, mature colonies (Shibao et al. 2010). By removing antennae of female vivipara and exposing them to different densities, researchers found that tactile cues are a key mechanism that regulates soldier production because soldier production was reduced in females without antennae, even at high densities (Shibao et al. 2016). However, females without antennae still produced a higher proportion of soldiers at high densities than controls at low density, suggesting that the post-natal experiences of intact nymphs born by the antennae-less females likely affect soldier production. In effect, the nymphs can developmentally rescue the missing signal from their antennae-less mothers (Shibao et al. 2016). The story with *T. styraci* is more complex than simply tactile cues alone. Remarkably, in *T. styraci*, the density effect depends on caste: density has a positive effect on soldier proportions when only

normal nymphs interact with one another, but has a negative effect when normal nymphs come in contact with soldiers (Shibao et al. 2004a, b).

Clearly, more than tactile cues are at work in caste regulation in species like *T. styraci*. Although it is likely that endocrine mechanisms are important in caste regulation in aphids, at the moment very little is known. The patterns are likely to be complex, as there is a great deal of variation in aphid social structures and how soldiers are produced and presumably regulated (Fig. 2). First-step questions include whether developmental fates governed by the same mechanisms in species that monomorphic soldiers compared to those that produce dimorphic soldiers? Are the mechanisms the same or different on primary and secondary host plants, and do they vary across species with different social life histories (Fig. 2)? Are conserved pathways shared between aphids and higher social insects? Recent work has shown an important role for the neuropeptide hormone corazonin in inducing hunting behavior and inhibiting ovary development in *Harpegnathos* ants, and likely other social insects as well (Gospocic et al. 2017). Corazonin is a ubiquitous regulator of response to stress in insects, expressed in the CNS. Remarkably, in the eusocial aphid *Pseudoregma bambucicola*, a structurally related adipokinetic hormone and its receptor exhibit caste specific expression on both the primary and secondary host plants (Jedličková et al. 2015). Adipokinetic hormones are involved in lipid metabolism and other stress-induced energy demands for energy mobilization (Gäde 2009). These results suggest the possibility that insect neuropeptide hormones that share evolutionary and functional similarities have been convergently recruited into caste regulation in social insects. Whether aphids will contribute to such insights requires a complete social aphid genome, but at the moment we must wait. While there are genomes for the pea aphid and other crop pests in the Aphidinae, the divergence between these species and social species places a limit on the usefulness of the genomic references for studies of sociality in aphids. Mechanistic studies of caste regulation will be greatly advanced with the publication of the first genome of a social aphid.

Defense Traits for herbivory may serve as pre-adaptations for defense against exploitation. In many species, soldiers use their stylets to puncture the cuticle of insect invaders in a manner that is similar to how they probe plants. For example, soldiers of at least one aphid species attack insect predators with their mouthparts and secrete a biologically active, mid-gut derived venomous protease, implying that social aphids can redeploy digestive enzymes for defense against predators (Kutsukake et al. 2004). There are likely diverse biochemical adaptations for defense in aphids (Kutsukake et al. 2008). For example, in the eriosomatine *Pemphigus obesinymphae*, soldiers appear

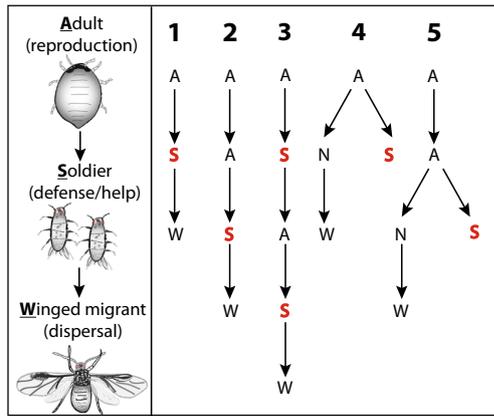


Fig. 2 Examples of the variation in aphid social organization across the Eriosomatinae and Hormaphidinae. On the left, the main life stages are indicated (reproduction, defense and dispersal). On the right are five different group structures, although there are additional varieties. Each arrow is a different generation within a group, and the soldier morph is shown in red. For example, in #5, soldier morphs do not appear until the 3rd generation, and there is a dimorphism between normal juveniles and soldiers. F = foundress; W = winged migrant; A = apterous female; N = normal, non-soldier; S = soldier. Detailed descriptions can be found in Blackman and Eastop (1994); Stern and Foster (1996); Aoki and Kurosu (2010)

to induce an immune reaction when they attack larval flies with their needle-like mouthparts (Lawson et al. 2017), an effect that may underlie their lethality (Lawson et al. 2014). In addition to simply wounding their victims, one explanation is that soldiers secrete factors that have toxic, immunological effects, such as effector molecules, symbionts, or viruses. This is intriguing because the key to success of all aphids on plants (social or not) is their ability to disrupt plant immune responses, principally via the secretion of enzymes, molecules and peptides with proteolytic or inhibitory activities (Will et al. 2013). Perhaps the traits for overcoming plant resistance can also be used to antagonize insect immune responses, thus setting the stage for the evolution of effective soldiers.

It is also worth noting a few novel, chemical-ecology related manipulations associated with gall induction by aphid species and defense of the gall. Soldiers have been shown to repair holes bored into their gall using oral secretions; this scab formation and wound healing appear unique among insect herbivores and allows the colony to protect their resource (Kutsukake et al. 2009). Another, even more remarkable solution that has evolved involves manipulating the host plant to remove the excess liquid from honeydew. In this solution, aphids manipulated the plant to perform “plant-mediated waste removal,” in which the inner surface of the gall is specialized for absorption and removes aphid-produced honeydew from the interior of the gall (Kutsukake et al. 2012). These examples highlight the manipulative ability of gall-inducing aphids and emphasize the strength of pressures that select for maintenance and protection of their gall.

A Case Study on Chemical Defenses and Sociality in Social Aphids

Unlike the social Hymenoptera, aphids lack a stinger, and therefore there is no obvious exocrine source for biologically active compounds for defense. Rather, for those aphids that attack predators with their stylets, a parsimonious hypothesis is that, if aphids use chemical defenses, then those compounds that are either acquired from their host plants in feeding or living on hosts plants are involved, as in the case of gall repair (Kutsukake et al. 2012). We were curious whether plant-derived metabolites could be used by social aphids in defense against predators, and hypothesized that, if so, host plants might exert bottom-up effects on evolution of social traits in herbivorous insect species that express complex forms of sociality (in this case, on defense traits). Social aphids that induce galls may be particularly likely to use plant metabolites in defense of the gall, because of the unique ability of gall-inducing insects to manipulate plant chemistry (Nyman and Julkunen-Tiitto 2000; Tooker et al. 2008; Tooker and De Moraes 2009).

Recent discoveries have established the presence of lipids, lipophilic molecules, and fatty acids in plant sap (Madey et al. 2002; Benning et al. 2012; Guelette et al. 2012). In animals, fatty acids are known to have insecticidal properties and act as immune adjuvants, and the enzymes that hydrolyze phospholipids are common components of vertebrate and invertebrate venoms (Fry et al. 2009; Ramsewak et al. 2001; Sivakumar et al. 2011). The pharmacological effect of such enzymes is due not only to their effects on membranes, but also to the bioactivity of free fatty acids themselves (Kini 2003). Termite soldiers, for example, express free fatty acids in their defense glands (Prestwich 1984). We focused on fatty acids, and asked whether they could be candidates for biologically active defense chemistry in social aphids.

We performed two sets of preliminary experiments with the North American social aphid *Pemphigus obesinymphae* (Aphididae: Eriosomatinae) and a closely related species, *Pemphigus populi-caulis*, that is less aggressive towards predators, and lacks several life history traits nominally associated with sociality in the genus (“non-social”, Lawson et al. 2014). Both species form galls on the poplar (*Populus deltoides*) in North America. Poplars respond to aphid feeding with an array of defensive chemicals, including phenolic compounds, proteinase inhibitors, chitinases, and polyphenol oxidases, some of which are found in phloem (Philippe and Bohlmann 2007). Predators of these species are mostly other insects such as chamaemyiid fly larvae, minute pirate bugs (Anthocoridae), and larvae of coccinellid beetles (Wilch 1999).

In the first experiment, using *Drosophila melanogaster* (Dmel) larvae as surrogates for chamaemyiid fly larvae, we sought to determine whether plant-derived compounds moved

from aphid to attackers. We collected galls of *P. obesinymphae* and introduced a 3rd instar *Drosophila* larva individually to seven galls. We allowed the aphid soldiers to attack for 20 min and then we collected the Dmel larvae and attacking 1st instar soldiers. We also collected some of the remaining non-attacking aphids, which were stored separately. We used two controls: unattacked *Drosophila* larvae that had been placed in empty galls for 20 min, and Dmel larvae not placed in galls. Thus, for GC analysis, the experiment had the following five categories: 1) Dmel not placed in a gall; 2) Dmel placed in a gall without aphids; 3) Dmel placed in a gall and attacked by aphids; 4) aphids with Dmel that did not attack; 5) aphids that attacked Dmel larvae. In the second experiment, experimental categories for both species were the same as in the first experiment, but with the addition of a non-social aphid species and analysis of tissue from galls, petioles, and ungalled leaves. In both experiments, approximately 5 to 10 individual aphids were analyzed per trial via gas chromatography (GC) and coupled gas chromatography-mass spectrometry (GC-MS). We extracted samples with pentane and analyzed the resultant solution generally following the methods of a previous effort to isolate plant-derived secondary metabolites from aphids (Byers 2005). Identifications of chemical components were made with GC-MS in electron ionization mode comparing retention times and spectra with that of pure compounds, following methods described previously (Tooker and De Moraes 2009). All data were log-transformed, and distributions within treatment

groups were visually inspected for skew and outliers. Data were analyzed by standard least squares ANOVA on transformed data, and where necessary, followed by post-hoc analyses using the Tukey-Kramer procedure. All analysis was performed in JMP v. 13.0.

The results of the first experiment indicated the presence of very few plant-derived compounds generally. However, many samples contained relatively high abundance of long-chain fatty acids (FAs), including the saturated, myristic (C14:0), stearic acids (C18:0), and the unsaturated oleic acid (C18:1 cis-9). These compounds were abundant in 1st instar aphid nymphs and the Dmel they attacked (Fig. 3), suggesting that soldier aphids somehow translocate these three fatty acids to Dmel larvae. Notably, these fatty acids were not detected in the sample of aphids selected from the non-attacking group.

In the second experiment, although there was much variation in the data, both aphid species were enriched with the three FAs we identified previously (Fig. 4). Each FA was significantly more abundant in *P. obesinymphae* than in *P. populi-caulis* (stearic: $F_{1,54}$, $p=0.0012$; oleic: $F_{1,41}$, $p<0.0001$; myristic: $F_{1,54}$, $p=0.0013$), but there was no difference in the amounts of FAs in the gall tissues in the two species (stearic: $F_{1,8}$, $p=0.64$; oleic: $F_{1,8}$, $p=0.61$; myristic: $F_{1,8}$, $p=0.64$). Because previous work on other gall-inducing insects indicated that gall tissues tend to be enriched for fatty acids (Tooker and De Moraes 2009), we expected that poplar aphid galls would also be enriched

Fig. 3 GC-MS showing the abundance of fatty acids (FAs) in aphid soldiers and their victims, relative to controls (hand traced overlay of original chromatogram to improve readability)

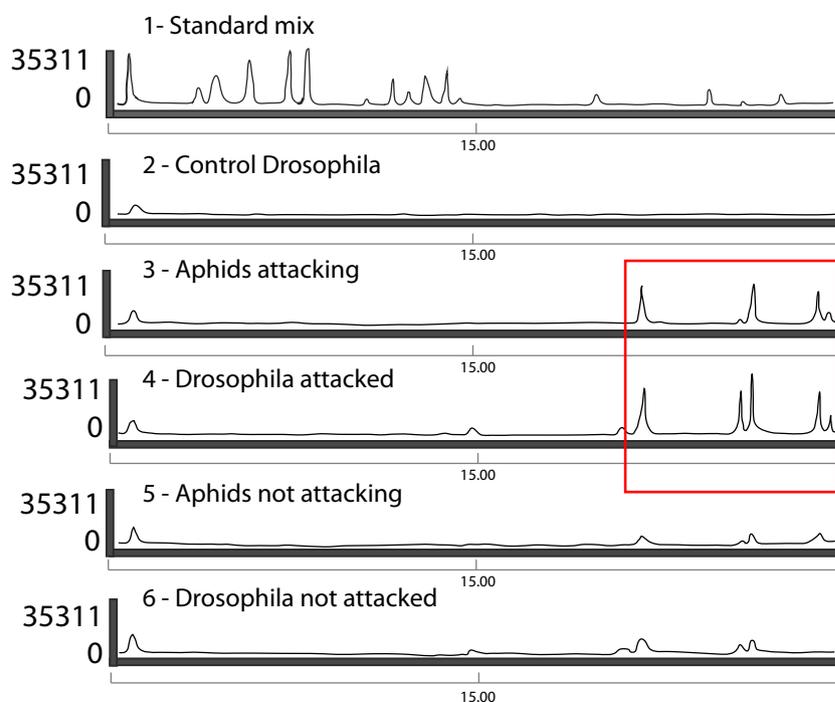
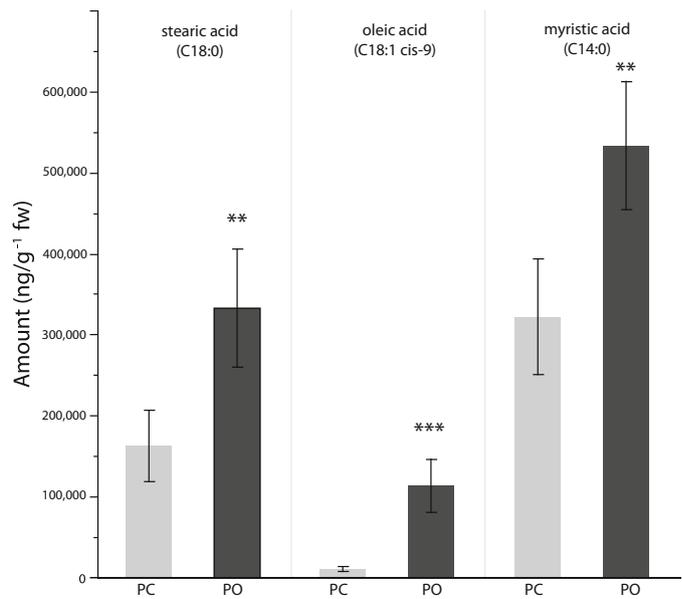


Fig. 4 Mean fatty acids (ng g^{-1} fw \pm s.e.) by aphid species. PO = *Pemphigus obesinymphae*. PC = *Pemphigus populi-caulis*. One-way ANOVAs on the log-transformed data. ** = $p < 0.01$; *** = $p < 0.001$

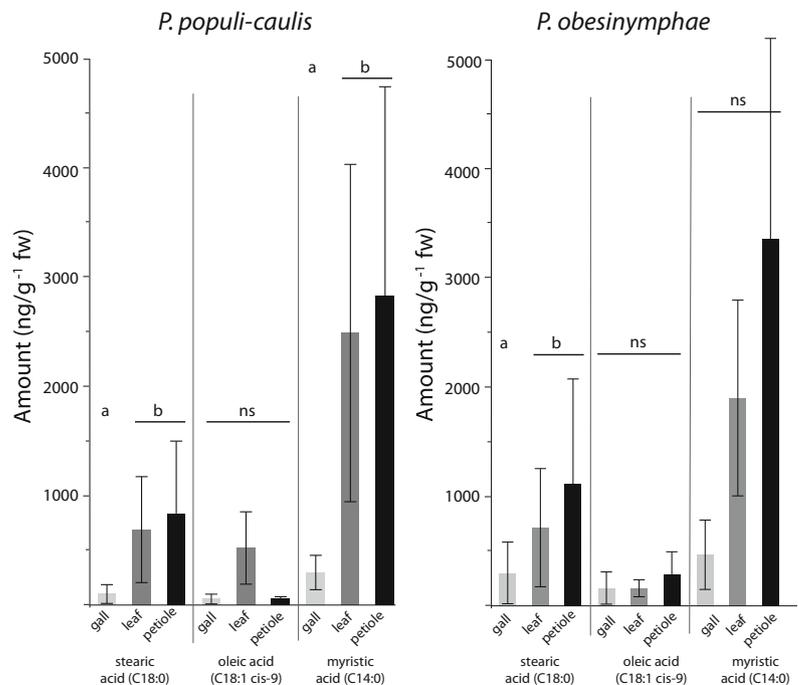


for FAs. However, relative to leaf and petiole tissue, FA amounts tended to be lower in gall tissue relative to surrounding leaf and petiole tissues, particularly stearic and myristic acids (Fig. 5; *P. populi-caulis*: stearic: $F_{2,18}$, $p = 0.0097$; oleic: $F_{2,15}$, $p = 0.055$; myristic: $F_{2,18}$, $p = 0.027$; *P. obesinymphae*: stearic: $F_{2,15}$, $p = 0.0441$; $F_{2,15}$, $p = 0.5328$; myristic: $F_{2,15}$, $p = 0.0692$). Overall, the pattern of variation in these FAs across plant and aphid tissues were similar, suggesting that the FAs we measured in aphids may have been largely plant derived (Figs. 4 and 5). Dmel larvae exposed to aphids appeared to be enriched for stearic and myristic, but there

was no difference between those exposed to the eusocial species and the putative “non-social” species with only weakly aggressive nymphs (Fig. 6; stearic: $F_{2,17}$, $p = 0.014$; oleic: $F_{1,7}$, $p = 0.36$; myristic: $F_{2, 17}$, $p = 0.016$).

Although sample sizes were small and there was much variation in the data, the results suggest that aphid soldiers are translocating either plant-derived or aphid-derived fatty acids to their victims when they attack. In effect, they create greasy wounds that may enhance the functional effects of their bites. Poplar galls are enriched for fatty acids (Tooker and De Moraes 2009), as are the aphids that induce them. It is unclear whether the free

Fig. 5 Mean fatty acids (ng g^{-1} fw \pm s.e.) by plant tissue. Different letters indicate significant differences. ns = non-significant



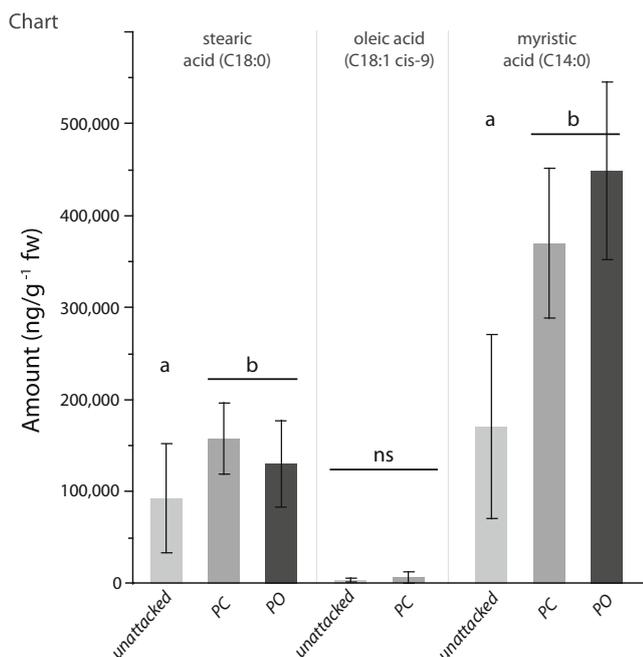


Fig. 6 Mean fatty acids (ng g⁻¹ fw \pm s.e.) in Dmel larvae after incubation with a social and non-social species, relative to unattached controls. Different letters indicate significant differences. There were not sufficient data to report for oleic acid. ns = non-significant

fatty acids we detected derive from the aphid poplar diet or are synthesized *de novo*, but the overall pattern of variation in FAs is remarkably similar between the aphids and plants, suggesting the possibility of a bottom-up, trophic movement of plant-derived metabolites from aphids to predators. Artificial diets have been developed for social aphids (Shibao et al. 2010), and it would be interesting to use these to characterize how social aphids use both primary and secondary metabolites in defense. The host plants of aphids and other herbivorous social insects (i.e., thrips; Abbot and Chapman 2017) may provide more than simply nutrition and nests, but rather biologically useful molecules in defense of kin.

Conclusions and Future Directions

Social aphids offer many promising opportunities to make two key advances in understanding the evolution of sociality. First, they offer the opportunity to characterize the interface between insect sociality, which is conceptually robust thanks to decades of comparative and theoretical work on many species (Akçay et al. 2015; Johnson and Linksvayer 2010; Rubenstein and Abbot 2017), and the regulation and development of insect polyphenisms, which is equally robust and primed for advance with the emergence of new functional tools (Brisson and Davis 2016). Second, they offer the opportunity

to ask novel questions about how complex sociality emerges out of a background of herbivory (Abbot 2015). The odd fact about sociality in aphids is that, once the full molecular mechanisms involved in the production of galls by aphids are elucidated (a major achievement), it will certainly shed light on the evolution of social behavior in aphids, because the two are inextricably intertwined (all social aphids are gall inducers). One of the central challenges in the study of insect social evolution is to understand the combination of shared and unique traits that collectively characterize the history of a particular social group (Toth and Rehan 2017). As we learn more about social aphids, we hypothesize that many novel features and traits will emerge. Aphids are sap-feeding herbivores, after all. What will be particularly interesting though will be convergence: it's a long way from aphids to ants and bees, and the molecular and chemical ecological features they share will have something interesting to say about the paths to sociality in insects.

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